Everything you always wanted to know about intransitive competition but were afraid to ask. Introduction to the special feature "Intransitive competition and species coexistence"

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Summary

- Over forty years after the introduction of the concept into ecology, intransitive (i.e., non-hierarchical) competition remains overlooked by ecological theory, despite theoretical work showing it could be a major driver of species coexistence.
- This special feature presents six studies including models, reviews, experimental studies and large-scale observational studies. Collectively, these studies help to: i) link intransitive competition with short- and long-term coexistence and with other ecological patterns, ii) evaluate the conditions under which intransitivity is more common and iii) determine how best to quantify the degree of intransitivity.
- The studies in this special feature show the generality of intransitive competition in nature, explore interactions between intransitivity and other coexistence

mechanisms and illustrate the effect of environmental conditions (drought, shade, fertility) on intransitivity and coexistence. They also show which metrics best quantify intransitivity and highlight the importance of adopting a more continuous view of competition as varying from strongly transitive to strongly intransitive. The studies also examine relationships between intransitivity and functional diversity and explore the evolution of intransitivity over time.

- *Synthesis*: The studies presented here advance the field by integrating intransitive competition into species coexistence and general ecological theory. We also highlight important research gaps that will hopefully inspire the next generation of studies in this topic.

Keywords: cyclic competition, community assembly, coexistence theory, competition, intransitivity, diversity, rock-paper-scissor dynamics

What is intransitive competition?

Competition networks are generally assumed to be hierarchical (transitive), with one dominant species excluding all others, the second most dominant competitor excluding all species but the first and so on. Coexistence between species, therefore, relies on: i) mechanisms which reduce competitive ability (fitness) differences between species (equalizing mechanisms), or ii) mechanisms that increase intra- relative to inter-specific competition, thereby resulting in stabilising niche differences between species (Chesson 2000; Adler, Ellner & Levine 2007). However, competition can also be non-hierarchical, or intransitive. Intransitive competition means that there is no single best competitor and, just as in the game of rock-paper-scissors, all species can beat some competitors while all lose to some others, i.e. there are "competitive reversals". This could allow species to stably coexist even without niche differences (Huismann & Weissing 1999; Wootton 2001, Laird & Schamp 2006). Intransitive competition was first explored theoretically by May & Leonard (1975) and Gilpin (1975), and since then a few studies have tested for the occurrence of intransitive competition and its effects on coexistence, developing different indices to measure it (see reviews in Aarssen 1992; Gallien 2016). However, the field has been dominated by modelling approaches or small-scale, single site experiments, meaning we still know very little about how often competition is intransitive or what conditions favour this type of competition.

How common is intransitivity?

Intransitive competition could be generated by a range of different ecological mechanisms. One possibility is a trade-off between resource competition and the production of species-specific allelopathic compounds: such as the one observed for three *Escherichia coli* strains, which compete intransitively because strain S overgrows

66 strain R, R overgrows C, but C kills S by releasing colicin, to which R is resistant (Kerr
67 *et al*. 2002, see also Durret & Levin 1997). Trade-offs in competitive abilities for
68 different resources could generate intransitive networks in similar way (summarized in
69 Aarssen 1992, see also Allesina & Levine 2011; Gallien 2016). Competitive reversals
70 from a strong hierarchy can also be caused by predators (LeBrun 2005), plant-soil
71 feedbacks (Lankau *et al*. 2011), or by the microclimatic changes produced by larger
72 species belonging to the same trophic level (e.g., nurse plants affecting competition
73 between understorey species via shading and an increase in environmental
74 heterogeneity: Soliveres *et al*. 2011, Aschehoug & Callaway 2015). Finally, the
75 existence of spatial structures and competition-dispersal trade-offs (Edwards &
76 Schreiber 2010; Ulrich, Jabot & Gotelli 2017; Yitbarek & Vandermeer 2017) can also
77 enhance intransitive competition.

78 Many mechanisms are therefore able to drive intransitive competition, which
79 might imply that it is likely to occur in nature and, indeed, intransitive competition
80 networks have been observed among intertidal organisms (Buss 1980), plankton
81 (Huisman & Weissing 1999), lizards (Sinervo & Lively 1996), bacteria (Kerr *et al*.
82 2002), lichens and bryophytes (Dormann 2007; Bowker, Soliveres & Maestre 2010) and
83 vascular plants (Freckleton & Watkinson 2000; Soliveres *et al*. 2015; Godoy *et al*.
84 2017). However, despite the increasing body of evidence supporting the generality and
85 potential importance of intransitive competition in nature, it has long been treated
86 mostly as a curiosity rather than as a major mode of competition. Indeed, studies on
87 intransitive competition are uncommon, and most work on coexistence has ignored it
88 (Fig. 1). One factor that has slowed the incorporation of intransitive competition into
89 general ecological theory has been the difficulty of measuring intransitivity in the field.
90 Improved metrics of intransitivity are therefore important to allow us to determine the

circumstances under which intransitive competition is more likely to arise, and what its consequences are for community-level patterns.

What is this special feature about?

Collectively the studies presented in this special feature aim to foster research on intransitive competition by addressing the drivers and consequences of this type of competition in natural communities, linking it with general coexistence theory and evaluating how to best measure and study it. If the reader ever asked the questions: i) how can we measure intransitivity? ii) how does intransitive competition affect coexistence? iii) what are the consequences of intransitivity for community structure? iv) what factors determine whether species compete intransitively or transitively? or v) How do intransitive competition networks assemble? This special feature should hopefully go some way towards answering them.

A short story of a difficult task: how can we measure intransitivity?

Quantifying the degree of intransitivity in multi-species competition networks is challenging and there have been a large number of different approaches taken to measure intransitivity and its effects on species coexistence (reviewed in Ulrich *et al*. 2014; Levine *et al*. 2017). Put simply, most of these metrics use pairwise competition matrices to assess the number of competitive reversals (or cycles) occurring across the whole network, or the proportion of n-species combinations that show competitive reversals. In this feature, Laird & Schamp (2018) provide the first assessment of the performance of these different metrics and conclude that those based on 3-species combinations are best to assess short-term (transient) coexistence (i.e., time to the first extinction). They also show that long-term (stable) coexistence is most strongly affected

by a very simple measure: the presence of an "unbeatable species" in the community. Whether or not such unbeatable species are common in nature is an interesting research gap to be addressed in the future. While nicely reviewing the existing metrics available to measure intransitivity and their performance, Laird & Schamp (2018) also reveal a crucial difference in the effects of intransitive competition on short- vs long-term coexistence, which could be important in understanding relationships between intransitivity and diversity in observational datasets. It is difficult to find generalities in studies using very different approaches, as conflicting results are as likely to be driven by different metrics of intransitivity as by differences in the way the target species compete. Studies comparing different methodologies, such as the one by Laird & Schamp (2018), are therefore essential if we are to draw generalities from existing literature.

Most metrics of intransitivity consider competitive exclusion as a binary process: a species either wins or loses in competition. However, two of the studies in this special feature (Gallien *et al*. 2018; Ulrich *et al*. 2018) show the need to consider more continuous measurements of competition (see also Gallien *et al*. 2017). If we take a more continuous view, there are almost endless possibilities for how a simple 3-species (A, B, C) competition network can organize, ranging from pure (or "strong") hierarchy (A >> B >> C, A >> C) to strong intransitivity (A >> B >> C >> A) and everything in between (e.g., A >> B > C = A, A >> B > C > A, A = B = C). Gallien *et al*. (2018) provide metrics that quantify the degree of intransitive competition in *n*-species combinations ($n \geq 3$) in a more continuous way, while, Ulrich *et al*. (2018) provide a metric, based on the “nestedness” commonly used in matrix algebra to measure intransitivity at the community scale.

In addition to the need for more continuous metrics, it has been recently argued that single intransitivity metrics can fail to adequately reflect the topology of intransitive competition networks or to capture the properties of those networks that affect species coexistence. A range of factors such as the connectance of each species with others (Alcántara *et al*. 2016), the number of species involved (Allesina & Levine 2011; Gallien *et al*. 2017), relationships between the competitive sub-networks existing amongst the different species within a community (Cheng *et al*. 2014), or the competitive ranking of each species (Laird & Schamp 2009; Soliveres *et al*. 2018) may play a role in modulating how a given level of intransitivity affects species coexistence. It is therefore important to use a range of metrics to quantify these different aspects of intransitivity, or at least to consider the different ways in which intransitivity can affect coexistence when interpreting a given metric. The methodological advancements in this special feature will undoubtedly help future studies to properly quantify intransitive competition and to address the circumstances under which it plays a role in the maintenance of biodiversity. Importantly, studies on intransitivity extend to disciplines other than ecology, with examples in law, economics and politics (Ziss 2007; Ludovic, Musy & Saidi 2012; Klimenko 2015), to name but a few. The metrics offered in this special feature will hopefully help to advance research within these fields too.

How does intransitive competition affect coexistence?

Early studies on intransitivity considered it a potentially important coexistence mechanism; however, work on intransitive competition has largely taken place outside the main body of coexistence theory (Fig. 1). "Modern coexistence theory" was developed by Peter Chesson and others and contains the key insight that species can coexist either by being similar in competitive ability (fitness) or by being different in

their niches (Chesson 2000). Coexistence theory typically assumes that competitive ability or fitness differences are hierarchical, however they could also be intransitive and coexistence models can be developed in which species fitness differences are intransitive (Godoy *et al*. 2017; Matías *et al*. 2018; see also Gallien *et al*. 2017; Levine *et al*. 2017; Saavedra *et al*. 2017).

The key question is then: *how important are intransitive fitness differences relative to niche differences in promoting coexistence?* Strong intransitivity can drive coexistence even without any niche differences between species, assuming that competitive ability differences are perfectly balanced (Laird & Schamp 2006; Allesina & Levine 2011), and most of the theoretical work on intransitivity has dealt with this case, although such a scenario could be rather uncommon in nature. Only two studies have so far looked at the interaction of weak intransitive fitness differences and niche differences, both suggesting that intransitivity alone is unlikely to promote stable coexistence (Gallien *et al*. 2017; Godoy *et al*. 2017). However, intransitivity could enhance opportunities for species coexistence and allow two species to stably coexist even in conditions where niche differences would otherwise be too small (Gallien *et al*. 2017; Godoy *et al*. 2017). Viewing competition in a more continuous way also shows that the strength of competitive differences between species affects whether intransitivity in these competitive differences can promote coexistence. Theoretical studies suggest that, if fitness differences are too heterogeneous, i.e. if some species pairs differ dramatically in fitness whereas others are similar, then intransitivity is less effective at promoting coexistence (Gallien *et al*. 2017; see also Soliveres *et al.* 2018). Future work therefore needs to more fully explore the roles of intransitivity, fitness differences and niche differences in promoting coexistence.

A further factor that may be important to consider is the number of species involved in an intransitive loop: a key result from theoretical studies is that intransitive competition loops formed by an odd number of species will stabilize coexistence whereas loops formed by even numbers of species will destabilize it (e.g., Gilpin 1975; Allesina & Levine 2011; Gallien *et al*. 2017). However, to the best of our knowledge, empirical support for this theory remains elusive. It also remains untested whether the relative importance of fitness differences (including hierarchical and intransitive ones) and niche differences, as drivers of coexistence, changes between communities with odd vs even numbers of species.

Species coexistence is likely to be largely driven by environmental heterogeneity, however very few studies have examined how environmental conditions affect niche and fitness differences or the degree of intransitivity. Matías *et al*. (2018) and Stouffer *et al*. (2018) are amongst the first studies to do so. Matías *et al*. (2018) show more intransitive competition under experimental drought conditions, confirming results from observational studies by Soliveres *et al.* (2015) and Ulrich *et al*. (2018). However, Matías *et al*. (2018) also show that an increase in intransitivity under drought is not sufficient to compensate for the reduction in niche differences that also occurs. This means that fewer species could actually stably coexist under drier conditions, nicely demonstrating that the drivers of intransitivity and of coexistence need not always align. Stouffer *et al*. (2018) also reveal significant differences in competition networks between sun and shade conditions, with shade providing unique coexistence opportunities for some species pairs. These results also provide a mechanistic basis for the observed influence of nurse plants on the competitive networks of their neighbours, by showing how shading can alter competitive outcomes (e.g., Soliveres *et al*. 2011; Aschehoug & Callaway 2015).

Another important extension for coexistence models is to consider temporal variation in species abundances. Most coexistence models assume a fixed-point equilibrium and calculate how many species can coexist at this equilibrium. The study by Stouffer *et al*. (2018) shows that this may underestimate the number of species that can coexist stably. These authors continue the work that Gilpin started back in 1975 and show that cyclic intransitive competition dynamics may have a large impact on stable species coexistence. Together, this study and the one by Ulrich *et al*. (2018) show that ignoring spatial and temporal heterogeneity may underestimate the degree of intransitivity present and the opportunities for coexistence. More studies determining how coexistence mechanisms are affected by environmental factors are therefore needed.

Research on species coexistence has mostly focused on single trophic levels but intransitive competition could occur at multiple trophic levels. A few studies have illustrated how higher trophic levels can disrupt competition hierarchies (i.e., by shifting them from hierarchical to intransitive; LeBrun 2005; Cameron, White & Antonovics 2009) and have highlighted the importance of considering "mesoscopic" interactions (i.e., interactions between competitive loops; Cheng *et al*. 2014) or multi-trophic stable coexistence (Godoy *et al*. 2018). Determining the extent of coupling between (in)transitive fitness differences across trophic levels is therefore emerging as a key new topic that could help us to better understand the mechanisms of species coexistence in complex communities.

Beyond species coexistence: what are the consequences of intransitivity for community structure?

Research on the consequences of intransitive competition for community-level attributes other than richness or species abundances is in its infancy. Changes in competition hierarchy have been related to spatial, functional trait and phylogenetic patterns (Gallien 2016; Maynard *et al*. 2017; Vandermeer & Yitbarek 2017). Reciprocal competitive advantages, necessary to cause intransitivity, can arise from trade-offs in competitive ability for different resources; and if functional traits are linked to competition then more intransitive networks should have higher functional trait diversity (Maynard *et al*. 2017; but see Gallien 2016). In this issue, Gallien *et al*. (2018) suggest strong links between intransitive competition and the evolution of greater functional trait divergences in a given clade, which is supported by the empirical, bivariate relationships found by Ulrich *et al*. (2018) in salt-marsh plant communities. Soliveres *et al*. (2018) also show that intransitivity is related to the functional traits not only of the target species but also of those with which it is competing (see also Kunstler *et al*. 2012). Interestingly, clear relationships between functional traits and competitive dominance have been observed in a number of taxa when competition is hierarchical (LeBrun 2005; Kunstler *et al*. 2016; Liouw *et al*. 2016; Miller *et al*. 2017), but a study in this issue suggests that these relationships may dampen when competition is intransitive (Soliveres *et al*. 2018). This opens the question of whether cases where traits fail to predict competitive ability could be indicators of intransitive competition. If intransitive competition is based upon contrasting competition hierarchies for different resources, then traits related to the acquisition of only one of those resources should be less predictive of the overall competitive rank of a species than if the competition hierarchy is consistent for all resources.

If intransitive competition affects functional trait distributions, then it could also affect other community/ecosystem properties. A couple of studies have shown effects

on invasion by exotic species (Henriksson *et al*. 2016; see also Gallien *et al*. 2018) and diversity-function relationships (Maynard, Bradford & Crowther 2017). It has not been until this decade that ecologists have started to investigate how the ways species compete can affect the patterns that emerge at the community-level. The new methods being developed to assess intransitive competition, and the slow but steady increase in the number of studies in this topic, will certainly provide novel insights into the ways in which intransitive competition affects community attributes and ecosystem functioning.

What factors determine whether species compete transitively or intransitively?

Despite the relatively low number of studies on the topic, and the variety of approaches that such studies have undertaken, we are starting to gather some generalities on what factors drive intransitive competition (Table 1). Amongst environmental factors, it has been suggested that both productivity and heterogeneity should enhance the degree of intransitivity in competition. Theoretical approaches suggest that intransitive competition is more likely in heterogeneous environments (Allesina & Levine 2011; Schreiber & Killingback 2013), where reciprocal competitive advantages (competitive reversals) may disrupt competition hierarchies. A study within this special issue reports the first empirical evidence for this (Ulrich *et al*. 2018). Gilpin (1975) also suggested that intransitive competition should prevail in productive environments, especially in the tropics; however, in this issue Matías *et al*. (2018) and Soliveres *et al*. (2018) refute this hypothesis using a variety of approaches. These three studies show more intransitivity under drier or unfertile conditions, meaning they find, in fact, that competition tends to be more hierarchical under fertile and productive conditions (see also Soliveres *et al*. 2015). This has important implications for understanding effects of global change on biodiversity, as changes in productivity or heterogeneity following

land use or climate change could alter the nature of competition and therefore opportunities for coexistence.

The characteristics of the competing species will also strongly determine whether or not they engage in intransitive or hierarchical competition (see *Beyond species coexistence: What are the consequences of intransitivity for community structure?* above). Amongst these species-specific traits, mobile organisms seem less likely to compete intransitively than sessile ones (Reichenbach *et al*. 2007). Evidence for this idea is mostly indirect, with studies on mobile taxa including protists (Carrara *et al*. 2015), ants (LeBrun 2005), flies (Ulrich *et al*. 2014), fish (Henriksson *et al*. 2016) and birds (Miller *et al*. 2017) showing competition to be strongly hierarchical, whereas studies on sessile organisms more often show intransitive competition (Buss 1980; Dormann 2007; Bowker *et al*. 2010; Soliveres *et al*. 2015). However, it is easy to find evidence against this apparently general pattern, as shown by the first multi-taxa experiment testing this notion, published in this issue (Soliveres *et al*. 2018). In addition, mobile organisms, such as lizards or plankton, are paradigmatic examples of intransitive competition (Sinervo & Lively 1996; Huismann & Weissing 1999). Whether or not the effect of mobility on competitive networks is modulated by other traits, such as range size, the habitat where a species lives (spatially structured or not), or the way it competes (i.e. whether competition for space is important, as in intertidal organisms or lichens) remains to be studied.

How do intransitive competition networks assemble?

Environmental and species-specific factors may, therefore, modulate whether or not species engage in hierarchical or intransitive competition. But how do intransitive competition networks assemble in the first place*?* It has been argued that strong

313 intransitivity may not easily occur in nature as it requires the three species involved to
314 be present simultaneously (e.g., Gallien *et al*. 2017; but see Zhang & Lamb 2012;
315 Stouffer *et al*. 2018). In this special feature, Gallien *et al*. (2018) explore a potential
316 mechanism by which initially weak intransitive competition could strengthen through
317 time. The authors use theoretical models to explore how intransitivity could evolve in
318 sympatry, which is one of the first attempts to link intransitive competition to eco-
319 evolutionary dynamics (see also Vasseur *et al*. 2011; Lankau *et al*. 2011; Patel &
320 Schreiber 2015; Ehlers *et al*. 2016). The authors show that (weak) intransitivity emerges
321 in these models and tends to strengthen through time as species diversify, which
322 increase the resistance of the communities to invasion and slows further evolution.
323 Communities may also diversify during succession or community re-assembly, as
324 species shift abundances and phylogenetically or functionally distinct species come to
325 dominate communities (e.g., Allan *et al*. 2013) or as species evolve to differentiate in
326 their traits (Vasseur *et al*. 2011; Zuppinger-Dingley *et al*. 2014). The degree of
327 intransitivity might therefore also change as communities assemble, although this has
328 rarely been considered and theoretical predictions are lacking. One study showed that
329 intransitivity actually decreased during succession (Ulrich *et al*. 2016) but there is as yet
330 no consensus on how intransitivity might change over time, as communities assemble
331 and evolve.
332
333 **Conclusions and research gaps**
334 The papers in this special feature, and a growing body of evidence, show that
335 intransitive competition may be much more common than previously thought and
336 should therefore be incorporated into general ecological theory. Progress in the field has
337 been hampered by large inconsistencies in how we assess pairwise competitive abilities,

how we measure competitive reversals and intransitivity, and how we infer coexistence. This clearly limits our ability to extract general conclusions from the existing literature, and calls for further research aimed at reconciling results derived from these different approaches. The studies presented here use a range of approaches to quantify intransitivity and one of the key conclusions from them is that we need to broaden our view of what constitutes intransitivity beyond only "strong" intransitivity (full competitive reversals) to consider also more partial or "weak" intransitivity. This expanded view allows us to ask how competition varies continuously from transitive to intransitive along environmental gradients (or with global change) and through time. Studies within this special feature suggest that intransitive competition will be more likely under heterogeneous and unproductive conditions, and for those species relatively similar in their competitive abilities: future work is needed to determine how general this is. Comparisons of the various metrics also suggest that those based on 3-species combinations can be more informative than whole community metrics. Linking intransitive competition to coexistence is a major aim of this special feature and the studies here show that weak intransitive competition can enhance short-term coexistence, and that effects on stable coexistence can depend on interactions between intransitivity and niche and fitness differences. They also show that coexistence studies need to expand their focus to consider environmental variation and temporal variation in population sizes, i.e. multiple-point equilibria, as these will have large effects on intransitivity-coexistence relationships.

What are the main open questions? As highlighted above, we definitely need more empirical work evaluating: how general intransitive competition is in a range of systems, which factors drive it, how it combines with niche and fitness differences to drive coexistence and what consequences it has for community-level attributes and

ecosystem functioning. This is especially true for complex and realistic communities, including multiple trophic groups: research on multitrophic coexistence, let alone intransitive competition at multiple trophic levels, has hardly been done. Long-term studies, evaluating changes in competition over time, remain rare (see Ulrich *et al*. 2016; Gallien *et al*. 2018) and theory incorporating temporal change is also uncommon. A key frontier in intransitivity research is therefore to evaluate changes in intransitivity over time to ask how it develops as communities assemble and how intransitive competition interacts with evolutionary processes. It is our hope that the papers in this special feature will help to inspire the next generation of studies aimed at linking intransitive competition with other coexistence mechanisms, assessing its generality and the factors driving it, and evaluating the consequences of intransitivity for the structure and functioning of natural ecosystems.

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571 **Table 1**. Summary of the research gaps and generalities that can be drawn from the
572 contributions in this special issue and those of previous literature on intransitive
573 competition.

Increasingly well-supported evidence
-Intransitive competition has been observed in too many organisms to keep ignoring it.
-Methods based on triplets (3-species combinations, or cycles) seem to work best to measure intransitivity.
-We need to adopt a more continuous view of competitive interactions and see purely transitive or intransitive competition as extremes at the end of a gradient.
-Only strong intransitivity can allow coexistence in the absence of any other stabilising mechanisms but weak intransitivity can increase the range of conditions under which species can stably coexist.
- Competition tends to be more hierarchical under fertile than unfertile conditions.
- Intransitive competition is more likely in heterogeneous environments.
- Intransitive competition is more likely (or more likely to enhance coexistence at least) in communities with an odd number of species. Although, empirical support for this theory is lacking.
-The effects of intransitive competition on ecosystems may extend beyond species coexistence, with possible effects on spatial and functional trait patterns, resistance to disturbances, or evolutionary rates.
Research gaps
-How important are intransitive competitive ability differences compared to other stabilizing or equalizing mechanisms in promoting coexistence? Does this vary in a predictable way depending on species number (even vs odd number of species) or environmental conditions?
-Where along the continuum from strongly transitive to strongly intransitive do most natural communities lie? And how often are unbeatable species found in nature?
-Do the same ecological processes promote niche differentiation and intransitivity?
-How do intransitive competition networks emerge over the long term: do they frequently evolve in sympatry?

-What are the consequences of intransitive competition for functional trait distributions?

-Does the relationship between functional traits and competitive ability tell us anything about how hierarchical competition is?

-Is transient or short-term coexistence (time to first extinction, current diversity patterns) important and does intransitivity affect transient and/or stable coexistence?

-How does intransitive competition and the mechanisms promoting coexistence within a single trophic level extend to species from other trophic levels?

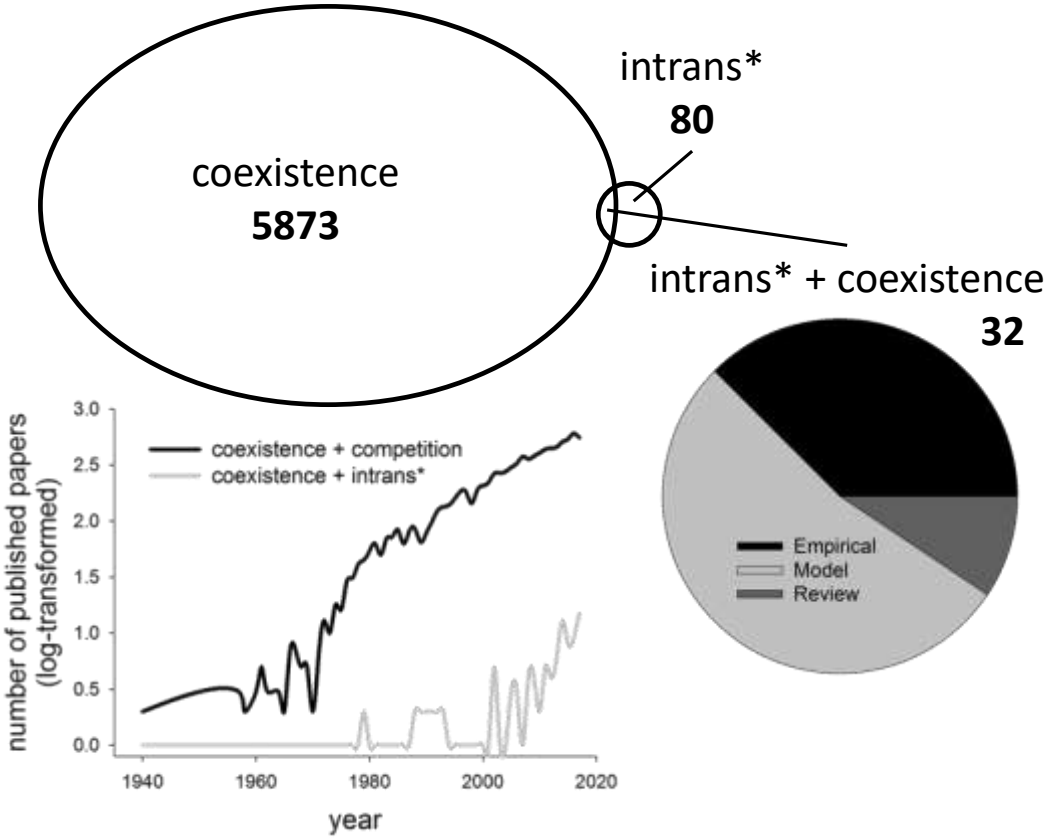

Figure 1. Bibliographic analysis showing the number of hits (log(x+1) transformed) for a search including "coexistence" (5873), "intrans*" (80), and both terms together (32) in the Web of Knowledge (accessed January 2018). The pie chart shows the dominance of theoretical (model approaches and reviews) studies linking intransitive competition to coexistence. The lines show the much larger number of papers published under the terms "competition" and "coexistence" (black) than those using the terms "intrans*" and "coexistence" (grey), which have experienced a sustained growth only since the year 2000 onwards.